

THE COURTSHIP DISPLAYS AND SOCIAL SYSTEM OF THE WHITE-RUFFED MANAKIN IN COSTA RICA

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ABSTRACT.—We studied the relationship between group and individual display in the courtship and social system of the White-ruffed Manakin (*Corapipo leucorrhoa altera*) in the Atlantic slope foothills of Costa Rica. Between 20 April and 28 May 1989, we searched for display logs and conducted 358 h of observations focused on four display logs. We found logs owned by a single resident male in which activity was continuous, as well as logs and areas where displays were occasional. Six of the eight logs found in the study area were arranged in two clusters separated by about 300 m, although we also found a solitary log 200 m from the nearest active display site. The resident male was at his display site 40.7–93.7% of the time, mostly alone. Residents were visited by other males mainly before 08:00 and less frequently by females later in the day. Residents continually gave advertisement calls during the day and performed several visual displays, including an elaborate *Flap-cheewah* in which the male would fly steeply upward from the display log to land explosively at high speed a few seconds later, instantly jumping while turning in the air to land facing the original landing point. Two of these displays culminated in copulations. Other common displays were a slow undulating Butterfly flight and Throat-flapping in which males slowly moved their heads, exposing the fully erected, contrasting white throat feathers. Males performed the displays alone, in the company of other males, or in the presence of females. We conclude that *C. leucorrhoa* displays in dispersed leks as found by other authors for *C. gutturalis*. Each log is owned by a single individual and the visits by other males may have a social function related to the establishment of a dominance hierarchy. We found important similarities between the two species of *Corapipo* and also with the genus *Masius*, which supports the proposed close relation between the two groups. Received 10 July 2001, accepted 12 March 2002.

The family (or subfamily) Pipridae, the manakins, is a Neotropical group closely related to New World flycatchers and cotingas, and currently is considered to include 40 species in 10 genera (Prum 1990). The group, in which all studied species show polygyny and lek/arena display, is best known for its variety of elaborate and peculiar courtship rituals performed by the males, which in most cases have much more colorful plumages than do females (Snow 1963, Sick 1967, Prum 1990). In lek breeding systems, males do not establish any lasting pair bonds with females. They defend nonresource-based display territories, the aggregation of which is defined as a lek (Bradbury 1981). According to the size of individual courts and the number of males in an aggregation, several types of leks have been identified in manakins: concentrated leks with usually >5 males aggregated, holding individ-

ual territories 1–5 m in diameter; dispersed leks, formed by 2–7 males holding territories 10–40 m in diameter; and solitary leks in which males holding display territories 10–30 m in diameter are isolated from others (Prum 1994).

The White-ruffed Manakin (*Corapipo leucorrhoa*) inhabits lower and middle levels of dense wet forests from southeastern Honduras to northwestern Venezuela. The species comprises three subspecies that differ slightly in the extent of white in the throat and primary feather morphology: *C. l. leucorrhoa* (Sclater) from Venezuela and Colombia, *C. l. heteroleuca* (Hellmayr) from Panama and southern Costa Rica, and *C. l. altera* (Hellmayr) from northern Costa Rica to Honduras, the subject of this study. Some authors consider *C. altera* from Central America and western Colombia to be a distinct species from *C. leucorrhoa* from eastern Colombia and Venezuela (Stiles and Skutch 1989, Wetmore 1972). Adult *C. leucorrhoa* males are glossy blue-black with a white throat patch; females and first year males are olive-green, usually with a grayish tint on the throat.

During their second year they are capable of mating (Aldrich and Bole 1937) and males have a distinct plumage, with a black mask and a partially white throat (Rosselli 1994). Females are heavier than males (12.5 g \pm 0.19

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SE, $n = 30$, and $11.1 \text{ g} \pm 0.09 \text{ SE}$, $n = 87$, respectively; Rosselli 1994), a characteristic that has been linked to displays in *C. gutturalis* (Théry 1997). The species is highly frugivorous and in Costa Rica its reproductive season extends between March and June (Skutch 1967, Rosselli 1994). The displays of the *altera* and *heteroleuca* subspecies of the White-ruffed Manakin were described by Aldrich and Bole (1937), Slud (1964), Skutch (1967), and Rowlett (in Davis 1982). Displays take place on fallen mossy logs in the forest, and include slow undulating flights between perches and approaching the display log, hops on the display log, flight song displays above the forest canopy, and a rapid, direct, noisy approach to the log in which a triple sound "Flap-chee-wah" (*sensu* Skutch 1967), partly mechanical and partly vocal, is emitted. Aldrich and Bole (1937) described the displays as solitary, while Skutch (1967) noted that several males could be present, but that each displayed independently. Rowlett (in Davis 1982) described several males displaying simultaneously, and Slud (1964) ascribed a high degree of coordination among the males. None of the authors saw a copulation or discussed the spatial arrangements of display logs, although Prum (1994) considered the display system of *C. leucorrhoa* to be a dispersed lek.

The other species in the genus, *C. gutturalis*, from northeastern South America, has been studied more extensively by Prum (1986) and Théry (1990, 1992, 1997; Théry and Vehrencamp 1995). This species is very similar to *C. leucorrhoa*, except for the presence of a large concealed white patch on the wing visible when the wing is extended (Prum 1986), the lack of shortened or emarginate outer primaries, and the inability to erect its throat patch into a ruff. *C. gutturalis* males display on mossy logs on the forest floor, arranged in exploded leks 120–250 m in diameter and 230–350 m apart, with a mean distance 38 m between logs of each arena (Prum 1986, Théry 1990). Males apparently hold individual territories more widely separated than in classical concentrated leks and perform competitive displays. In this species, groups of males were observed displaying together, with some of the individuals that displayed habitually in a territorial manner joining group display at other sites as well (Davis 1949, Prum 1986, Théry 1990). Prum (1986) inter-

preted this behavior as detached or mobile leks, in which "males abandon exclusive display territories for the competitive group display at a series of sites." More extensive observations by Théry (1990) led him to conclude that exclusive territorial behavior is more important than mobile group display, which he attributed more to a period of establishment of individual territories before the breeding period.

The objective of the present study was to examine the relationship between group and individual display in *C. leucorrhoa*. Specifically, we wished to determine whether *C. leucorrhoa* displays in mobile leks, as suggested by Prum (1986), or whether display logs have exclusive owners, as suggested by Théry (1990). For this study, we took advantage of a large banded population and a grid of study area trails from an earlier study on the annual cycle and fruit diet of this species (Rosselli 1994).

METHODS

We conducted the study at Finca el Plástico ($10^{\circ} 18' \text{ N}$, $84^{\circ} 01' \text{ W}$), a private reserve covered mostly by mature forest (premontane wet forest *sensu* Holdridge; Tosi 1969) 6 km south of Las Horquetas de Sarapiquí, Provincia de Heredia, on the Atlantic slope of Costa Rica. The reserve, along with its neighboring parks and protected areas, is part of a continuous forest area of nearly 44,000 ha that extends between elevations of 50 and 2,900 m. Annual rainfall is about 500 cm with a dry season between January and April or May, followed by rains during the rest of the year, peaking in July (for a more detailed description of the study site and bird community, see Rosselli 1989, 1994). We worked mostly in a 12-ha study area crisscrossed with a grid of trails 50 m apart, located in mature forest between 500 and 600 m in steep and varied terrain (Fig. 1). In a previous study (reported in Rosselli 1994), *C. leucorrhoa* had been one of the most abundant understory birds, and 179 individuals had been individually color banded at the site. We therefore did not use mist nets in the present study, hoping to disturb the birds as little as possible.

We spent 34 days in the field between 20 April and 28 May 1989, during which our main activities were censuses in search of display logs and detailed observations from blinds at active display logs. Censuses were conducted by three observers walking slowly along the trails in the study plot and stopping every 100 m for 30–60 min, listening for any call or sound produced by White-ruffed Manakins. Because of the intermittent nature of log activity, only by waiting ≥ 30 min at a site could we be certain not to miss finding any nearby display logs. Censusing was conducted intensively during the first week and periodically thereafter (9 days in all) to detect any new logs not found previously. We conducted censuses between 07:00 and

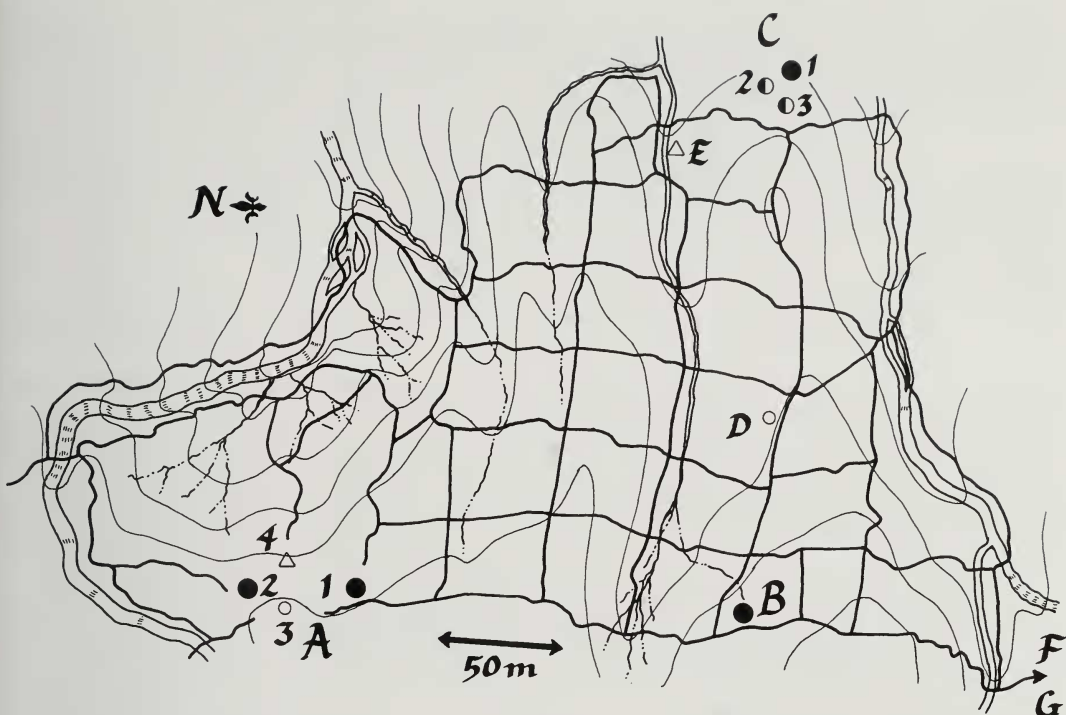


FIG. 1. Topographic map of 12-ha study area in Finca El Plástico (Heredia, Costa Rica) showing trail grid, and permanent and occasional display logs of White-ruffed Manakins (*Corapipo leucorrhoa*) and areas (contour lines denote 10-m intervals of elevation, between 520 and 590 m). Solid circles are logs with banded resident males, half-filled circles are logs with continuous activity but no banded male, open circles are logs without permanent activity, and open triangles are areas with occasional displays but no log. Note that most logs were found in two main clusters (A and C). Data are from 1989.

13:00 along 3 km of trails; each segment was censused 5–6 times. We made observations from dawn to dusk (05:00–17:30, though mostly between 07:00 and 15:30), from blinds constructed with PVC pipe, sheet plastic, nylon screening walls, and fiberglass roofing sheets, set up 4–8 m from the logs. We accumulated 78 h of censuses and 358 h of observations at the logs.

Similarity in appearance made it difficult to distinguish females and first-year males, therefore some green unbanded individuals were considered first-year males according to their courtship behavior and reaction of resident males to them. Only in a small proportion of the visits were we completely sure these green individuals were females, either because they had been color banded previously or because they copulated with a male. We considered as females the other green individuals that behaved in the “secretive” way typical of the banded ones and elicited a courtship response in the male or males present.

Although censuses and observations were conducted mainly in the study area, we also spent nearly 40 h exploring and observing outside the plot. Our observations were focused on four of the active logs (A1, 65.5 h; A2, 82.5 h; B, 78 h; C1, 31 h); each of the other logs was observed for 5.5–20.9 h. At the four

main display logs, we made video recordings with a Canon 8-mm XM-E708 camera. We completed about 4 h of recordings that contain most of the elements of the display behavior of *C. leucorrhoa*. With the help of F. G. Stiles we also obtained sound recordings of the more common vocal and mechanical sounds emitted by the manakins with a Uher 4000 Report-L tape recorder. Subsequently, sonograms were made from the recordings by J. W. Hardy at the sound laboratory of the Florida Museum of Natural History.

RESULTS

Description, density and location of display logs.—We found eight logs on the study area at which male *C. leucorrhoa* displayed (Fig. 1). Four of these logs (A1, A2, B, and C1) each had a resident banded male that remained in the vicinity from 41–94% of the time, mainly alone (Table 1). At two (C2, C3), there was continuous activity, but the possibly resident males were not banded so we could not confirm their presence, and at two more (A3, D), we occasionally observed *C. leucorrhoa*

TABLE 1. Behavior of White-ruffed Manakins (*Corapipo leucorrhoa*) at display logs during 5-min observation periods, El Plástico, Costa Rica, April–May, 1989. Female visits were directly related to the resident's time alone at a log, and inversely related to the rates of visits by other males and advertisement calls.

	Display log			
	A1	A2	B	C1
Time resident at log (%)	67.8	40.7	79.4	93.7
Time resident alone at log (%)	61.4	39.1	73.4	46.6
Female visits/h	0.2	0.1	0.2	0.1
Other male visits/h	0.3	0.8	0.5	2.5
Advertisement calls/h	25.0	27.7	34.0	109.7

displays, but no individual was seen regularly at the site. We also detected sporadic displays and/or display calls in two areas where no log was found (A4, E). In addition, we found two more logs (F, G) about 1 km south of the study area. These two "foreign" logs were separated by nearly 80 m.

Considering only the continuously active (permanent) logs, the log density in the study plot was 0.5 logs/ha and the mean distance between logs (all pairwise distances) was 182.8 m \pm 110.6 SD. Most of the logs and display sites in the plot were arranged in two main clusters (Fig. 1). The mean distance between logs within clusters was approximately 27 m. According to observations by LR and F. G. Stiles (pers. comm.), some of these logs (A2, B) had been used during previous years, and some others that had been active during the 1988 breeding season were not active in 1989.

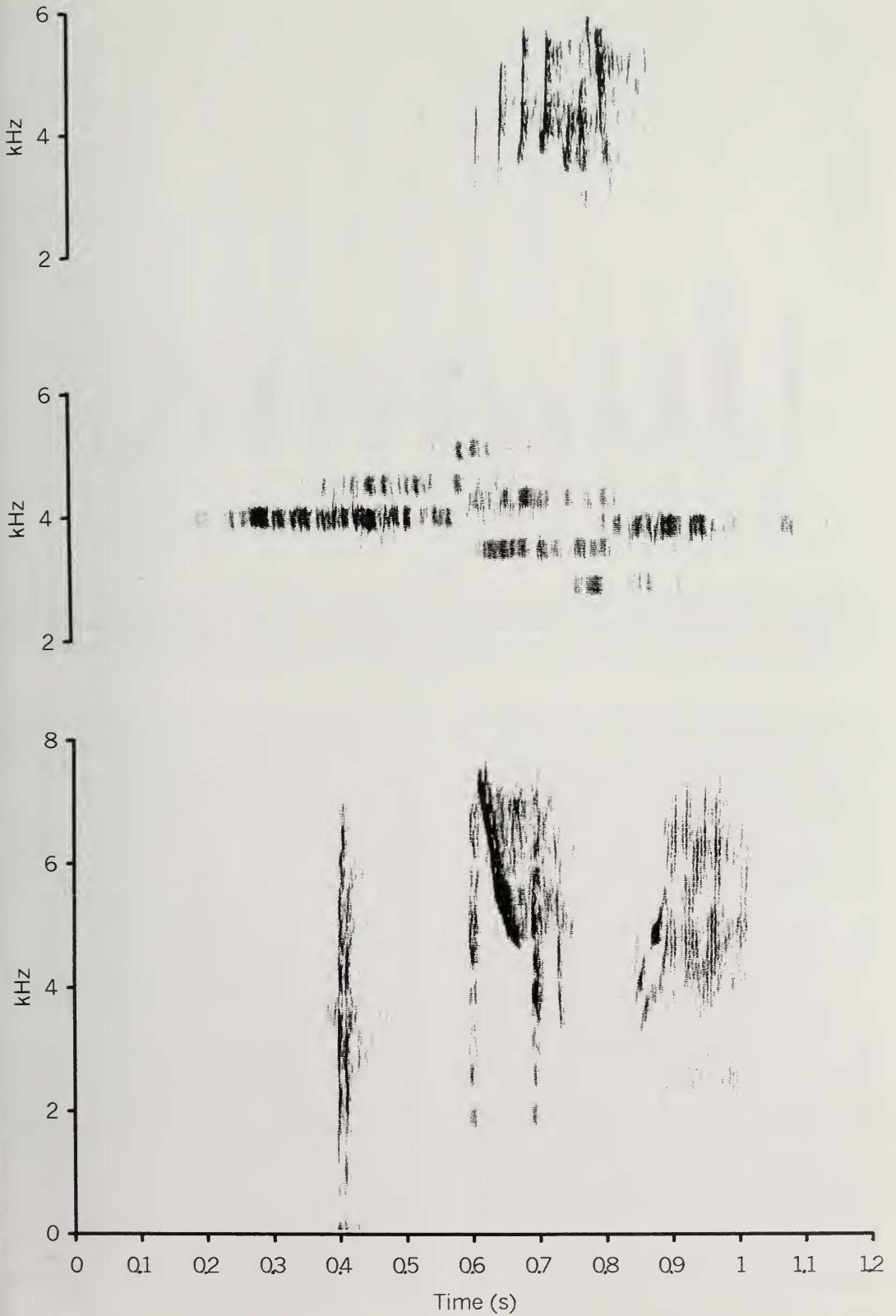
The White-ruffed Manakins displayed over horizontal portions of fallen trees or live lianas lying on the ground or \leq 40 cm above it. The total length of these logs and lianas (hereafter we refer to all simply as logs) ranged from 3.8 to $>$ 50 m (in some lianas that came down from the canopy). The manakins used specific, moss-covered portions of these logs, varying between 0.5 and 1.3 m in length. The diameter of the logs varied between 10 and 44 cm, and compass orientation was different for all of them. The part of the log on which the manakins displayed generally was clean and free of obstacles, except on one trunk, where a slender

(0.5-cm diameter) vine that the resident male frequently tried to remove crossed the display area perpendicular to the trunk. The manakins actively cleaned the logs by removing fallen leaves and debris, a behavior called "gardening" in other species (Snow and Snow 1985, Prum and Johnson 1987). The area immediately surrounding the logs was free of obstructions, but the configuration of the vegetation surrounding this display area was variable between logs. We found no visually consistent pattern of canopy foliage around the display logs, and no consistent pattern of fruit availability in the immediate vicinity.

Activity at the logs.—The activity pattern at the active logs was similar for the four logs observed at length. Each log was owned by a single adult male (the resident) that remained close to it most of the day from dawn to sunset. Although most residents remained by themselves most of the time, they all had almost daily visits from other males and, less frequently, from females (Table 1). When the resident males were alone at the log areas, they spent their time on 4–6 perches a few meters from the display area, regularly giving a high (3.7–6.2 kHz) short (0.28 s) trill "tree" note or advertisement call (Fig. 2a). This note also was given away from the display logs during feeding and by females. The rate of advertisement calls was 25–34/h, except for log C1 where calls were more frequent. Log C1 also was atypical in having a very high rate of visitation

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FIG. 2. Sonograms of White-ruffed Manakin (*Corapipo leucorrhoa*) vocalizations. (Top) Advertisement call or trill; (middle) warble or "nurr," possibly given by more than one male; (bottom) *Flap-chee-wah*. Recordings were made by F. G. Stiles, El Plástico, Costa Rica, May 1989. Sonograms were made on a Kay Elemetrics Model 7029A Sona-Graph, with bandwidth set at 300 Hz.



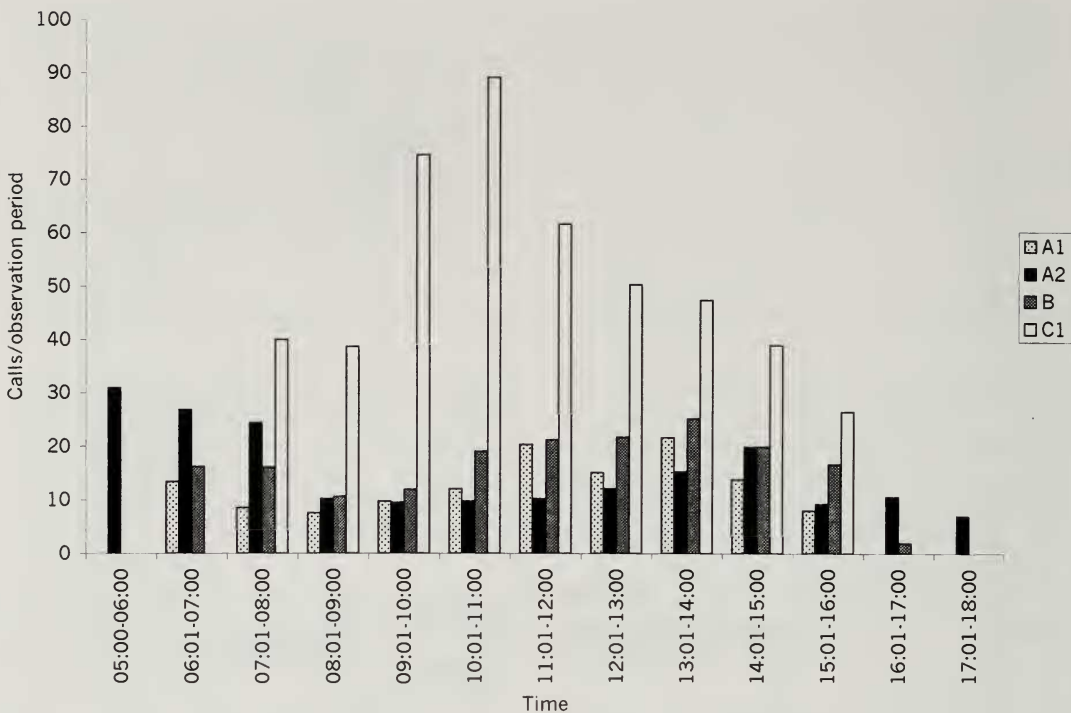


FIG. 3. Daily rhythms of calling intensity at display logs of White-ruffed Manakins (*Corapipo leucorrhoa*) on the study area, El Plástico, Costa Rica, April–May 1989. In three (A1, A2, and B) of the logs the numbers of advertisement calls per observation period was highest early in the morning and early in the afternoon. Log C1 was atypical in several respects, including the highest calling activity late in the morning.

by other males and, along with A2, the lowest rate of female visits (Table 1).

Resident males constantly moved between perches and frequently preened. They commonly left the area for short periods (generally <10 min), apparently to feed or bathe since they often returned with fruit in their bills or with wet plumage. The rate of advertisement calls through the day was similar for logs A1, A2, and B, with a peak early in the morning (06:00–08:00), a period of relative low activity between 08:00 and 10:00, and a steady increase thereafter until 14:00. At log C1 there was a pronounced peak between 10:00 and 11:00; we have no observations before 07:00 or after 16:00 (Fig. 3). The total number of calls on a single day ranged from 215 during 9 h of observation at log A1 to 1,377 during 8 h of observation at log C1. The rate of calls per observation period was <40 calls/h at logs A1, A2 and B, and 109.7/h at log C1 (Table 1).

Visits from other males, movements and associations.—The 200 observed visits from

males (other than the resident) at the display logs took place mostly in the mornings and mainly before 08:00 at logs A1, A2 and B. At C1, the number and rate of visits was much higher and peaked between 09:00 and 10:00 (Fig. 4, Table 1). The visits included males of different ages (first and second year, and adults) that usually came in groups of ≤ 6 individuals. Visiting males seemed excited and nervous, and displayed actively. The resident males sometimes took part in the displays. We also observed aggressive behavior between males (see below).

We heard one type of vocalization exclusively during these visits, when there was >1 male at the display log area. This was a longer trill similar to a warbling note “currrrrrrr,” between 2.5 and 5 kHz and up to several seconds in duration (Fig. 2b). When a group of males emitted this “warble” they stood very close to each other, sometimes only a few centimeters away on the same branch. We had the impression they were attracted to each other

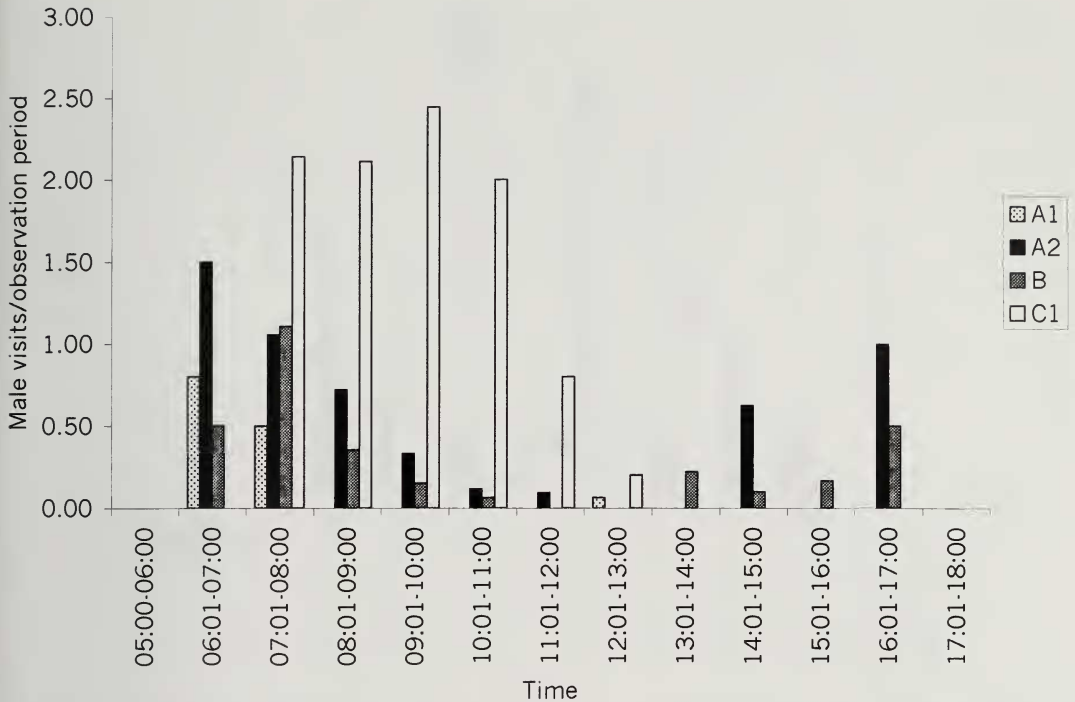


FIG. 4. Visits by nonresident males per 30-min observation period through the day at display logs of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989. Most visits occurred during early morning at logs A1, A2, and B, but at log C1 a very high visitation rate occurred during late morning.

while warbling. The resident male warbled with visitor males.

Besides numerous observations of unbanded females, young, and adult males, we detected 32 individually banded males (44% adults, 56% immatures) and 4 females during our observations. Twenty of these individuals (including the resident males of logs B and C1) were seen at only one of the display sites, seven at two sites, and five at three sites. Most of the movements between different display sites were made among adjacent sites; nine of the individuals seen on 2–3 different logs were concentrated in either the A or the C clusters, with maximum distances of 41 m and 11 m between logs, respectively. Three nonresident males made the longest recorded movements (300 m between B-0 and C1, 200 m between A2 and B, and 51 m between the E area and logs C3 and C2). Also, the resident male of log A1 occasionally visited logs A2 and A4 and displayed (see Fig. 1).

On 16 occasions we saw groups of males, including ≥ 2 banded individuals, visiting the

display logs; only three combinations of two banded males were seen together twice, the rest were different combinations of males in each cluster. Therefore, we found no indication that these were coherent groups. The visits to the logs lasted from < 5 min to > 5 h. We do not know where these visitors went later in the day.

At log A2, there were more visits at the beginning than at the end of the study. The resident started to spend much of his time at a new log (A3) 10 m away from the original one on the last days of our observations. The male displayed and was visited by a female at the new log.

Female visits.—“Females” visited all the active logs. We recorded 34 such visits to the four logs studied most intensively. Log A1 had the highest rate of female visits and logs A2 and C1 had the lowest (Table 1). Females visited the logs mainly between 09:00 and 15:00 when resident males were alone, except for log C1 where the few visits observed came

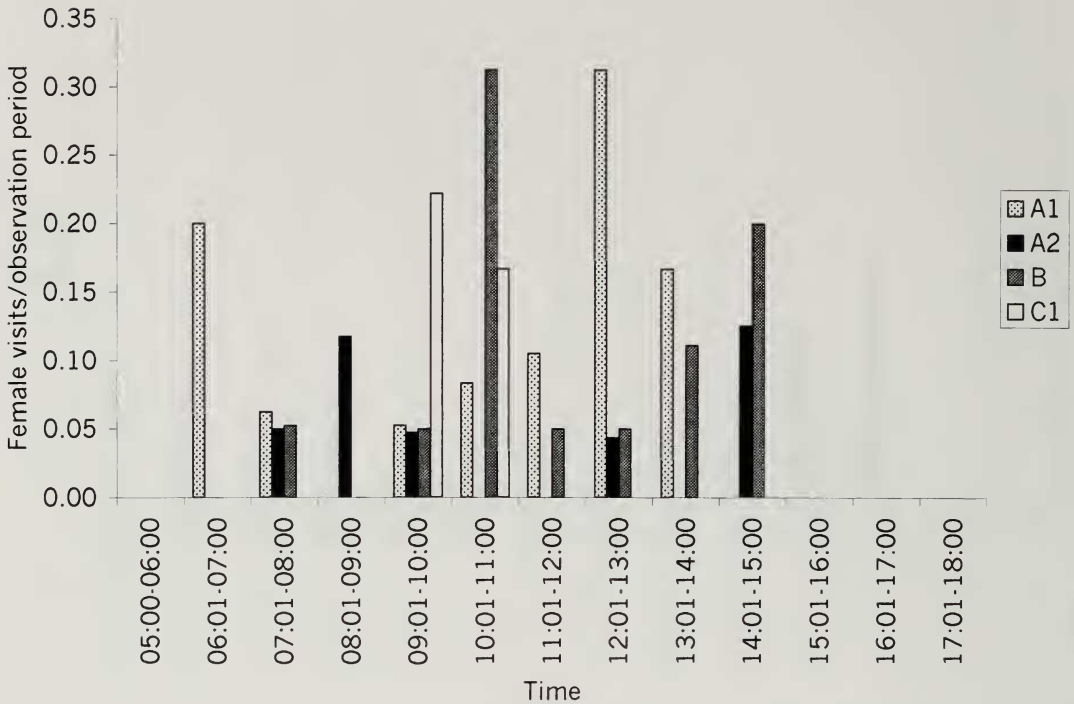


FIG. 5. Visits by females per 30-min observation period at display logs of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989. Most visits occurred 09:00–15:00 when there were few visits by nonresident males.

during a period of higher visitation by other males (09:00–10:00; Fig. 5).

Behavior at the display sites.—Besides perching around the log during most of the day and giving advertisement calls, resident *C. leucorrhoa* males performed several visual displays, some with associated sound:

Flap-chee-wah.—This was the most elaborate and spectacular display we observed. It was performed by resident males either alone or in the presence of females or other males. It also was performed by visiting males and, on several occasions, two or more males (including the resident) appeared to perform the *Flap-chee-wahs* in a coordinated manner.

In this display, the performing bird flew to the display log, then flew steeply upward, often in a spiral. At approximately the high point of the flight, 1–3 extremely high, thin notes (Canopy calls) were heard in about 34% of the times. We strongly suspect, judging from the far away quality of the notes and the fact that we invariably lost sight of the birds as they entered the canopy, that the birds flew straight up to above the canopy to give these

notes. About 2–3 s after giving these notes, the displayer plummeted diagonally down to the display log at very high speed and landed, facing the opposite direction from the ascent; instantly the bird jumped about 10–90 cm, turning in the air to land facing the original landing point (Fig. 6). After this second landing he sometimes remained crouched flicking his wings, or he sometimes immediately flew from the log. When another bird was perched on the log, the displaying male landed facing it in each case. At about the moment the bird first landed on the log a loud, explosive snap or “flap” noise was produced, followed immediately by one or two high notes (“chee” or “chi-chi”) and a sharp buzzing note (“waa” or “wheew”; Fig. 2c).

These notes were produced so rapidly, and the landing and jump were so nearly instantaneous, that it was impossible to determine exactly the relationship between the sounds and the jump. The “flap” apparently is a nonvocal sound, possibly produced by the modified primaries (Prum 1998); the “chee-waa” may be vocal. When a displaying bird landed on the

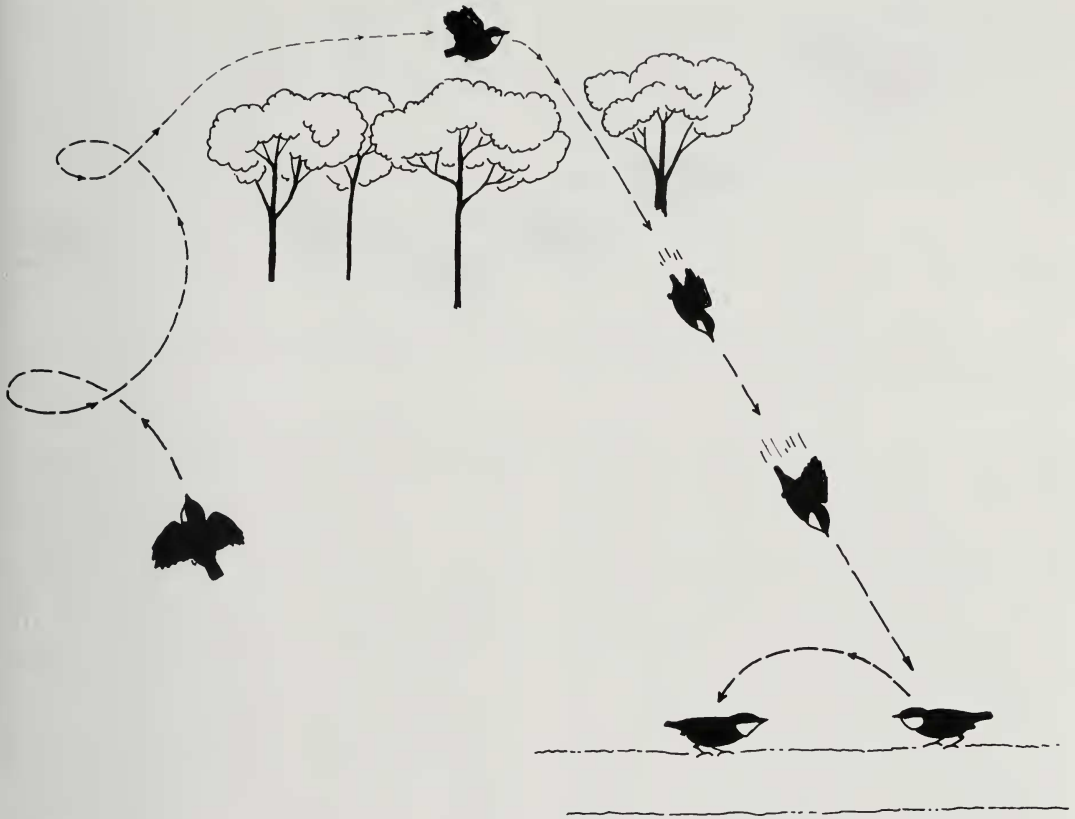


FIG. 6. Complete *Flap-chee-wah* display sequence of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989. Ascending flight, flight over the canopy with Canopy calls, and explosive landing on the display log and rebound (accompanied by “Flap-chee-waah” sound).

log following the jump, his throat feathers were strongly fluffed, but it was not possible to determine whether the throat was puffed out during the entire display. The directions of departure on the upward spiral, and arrival at the log, were constant on all *Flap-chee-wahs* performed at a given log. Generally a *Flap-chee-wah* was preceded by apparent nervousness, rapid flights between nearby perches, and landings on the display area of the log by regular flight or any of the special flights (Butterfly, Undulating) described below.

When several males performed simultaneous displays, the male that had landed in a *Flap-chee-wah* remained in a crouched position on the log, flicking his wings and looking up, as if waiting for the next male to land; when a second male landed, the original male usually flew away from the log and this second individual would remain on the log sim-

ilarly “waiting” for a third *Flap-chee-wah*. Sometimes the displaying males remained on the log and up to three males would be perched on the log at the same time. Rapid sequences of several *Flap-chee-wahs* were observed on several occasions with birds almost landing on top of each other.

Each element in the display (nonvocal sounds, vocal sounds, spiral ascending flight, rebound, Canopy calls) could be present or absent on a given occasion. The elements more commonly present were a landing at the log, followed by an upward flight, and the explosive landing with the *Flap-chee-wah* sound.

We detected no differences in the performance of displays between adult resident males and young visiting males; both performed complete display sequences and incomplete “practice” displays in which the calls or nonvocal sounds were different or the

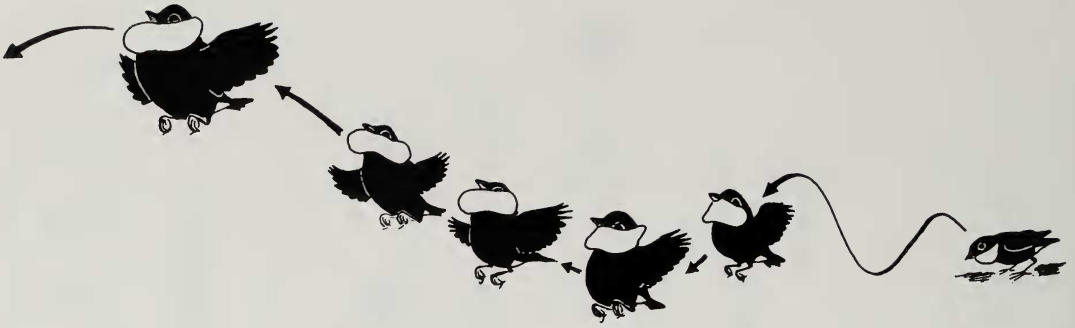


FIG. 7. Butterfly flight based on video images of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989.

jump was slow. Once we saw an immature individual crashing against some leaves in a display attempt at log G. We observed a total of 252 *Flap-chee-wahs*. Most (66.3%) of these displays were performed by 12 banded males, including the banded residents (56.7%). On 77 occasions the display was performed by unbanded adult males and 8 times by unbanded green individuals.

Butterfly flight.—This is a very stereotyped flight performed by males flying to or from the display log, or between low perches nearby. The flight is slow and undulating, the body held in vertical position with the plumage fluffed; in particular the throat is fully puffed out (Fig. 7). The Butterfly flight was almost always associated with the presence of a female or other males in the display area. No sound was emitted during this display; in fact, the flight was notably silent, the birds seeming to float like little black and white pompons.

Undulating and Rapid flights.—Another flight that probably was a variant of the Butterfly flight was the Undulating flight in which males would oscillate up and down, although with less pronounced waves and their body

and plumage in normal position. Sometimes the birds also performed straight Rapid flights nervously between the display log and nearby perches. Frequently before or after these Rapid flights males emitted a loud or subdued snapping sound “plop” or “flap” either in flight or on a perch. This sound was nonvocal, and probably produced with the wings, and also could occur as a single event or in association with other displays.

Throat-flagging.—This display consisted of a slow, stereotyped head movement performed by males perched on the display log, evidently to show off the throat feathers, which were fully erected to form a dense beard (Fig. 8). Facing diagonally toward the center of the log, with his head held low and horizontally, the male slowly rotated his head sideways through an angle of about 30–45°, so that one eye faced diagonally downward toward the log, the other diagonally upward; this head movement was accompanied by a single rapid flicking open-and-closed of both wings. The male then would repeat the head movement in the opposite direction. This display usually was performed following a But-

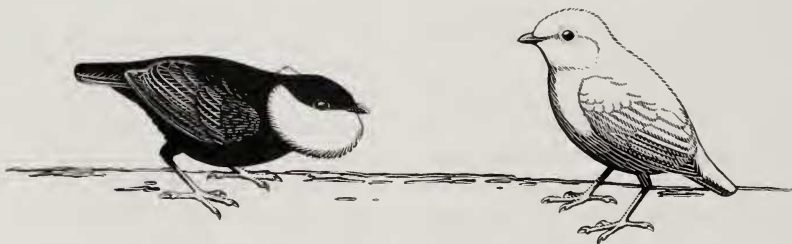


FIG. 8. Throat-flagging display performed on display logs by male White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989.

terfly flight, but also sometimes following *Flap-chee-wahs* or Rapid flights; it usually was directed at other birds (males or females) but occasionally was performed in the absence of other birds as well.

On many occasions a male, usually alone, was seen to move his head as if looking at the log with one eye and then the other, or look down as if looking at his feet, but not in the slow, stereotyped way described above and without the erected ruff. We believe this might be a variant of the Throat-flagging. Occasionally the residents displayed without any obvious reason.

Courtship of females and copulation.—The female visits to the logs lasted from a few seconds (in which cases the females probably were merely passing through the area) to >10 min, when they were visibly interested in courtship. The females typically arrived quietly, perching at heights ≤ 1.5 m on vertical stems of shrubs or saplings in the understory. Males reacted to their presence with fast movements and numerous Rapid and Butterfly flights to the display log or between perches. After each landing the males performed the Throat-flagging display. The female then began to follow the male on some of these flights, sometimes appearing to chase him. If the female landed on the log, the male continued with Rapid flights and Butterfly flights to and from the log for ≤ 12 min, each time landing 10–20 cm in front of her and Throat-flagging. During these periods we recorded 16–46 Rapid flights and 6–70 Butterfly flights. Finally, with the female perched on the central part of the display area on the log, the male would depart in the upward Spiral flight; the high thin *tsee* notes or Canopy calls were heard from above 75% of the times (compared to 34% when there was no female present), and the male would land with a *Flap-chee-wah*. If the female still remained on the log, he would land on one side of her, jump over her and land on the opposite side, then immediately hop toward her and mount; copulation lasted only about 2–3 s, then the female flew away.

We observed two sequences that terminated in copulations: one by the resident male at the C-0 log on 1 May the other by an unmarked adult male, presumably the resident, at the F log on 23 May. In both cases no other males

were present and the sequence of displays was as reported above. Many other sequences we observed did not end in copulation because the female departed. The female would abandon the area at any point of the described sequence; in several cases, she departed after the male had flown up toward the canopy during the final *Flap-chee-wah*.

Both copulations occurred relatively late in the day (12:45 and 14:47, respectively); indeed, most female visits occurred after 09:30 when the resident males were alone. The presence of other males, as often occurred early in the morning, might have disrupted courtship activities. We noted an apparent example of this several minutes after the copulation at log F. About 5 min after the copulation, a presumed second female arrived. The male performed several Butterfly flights, and the female landed on the log. When the male flew up to perform a *Flap-chee-wah*, a second-year male landed on the log in front of the female and performed the Throat-flagging display to her. At that moment the first male landed and the three individuals flew away; a similar situation was described by Davis (1949) for *C. gutturalis*.

If a female visited a log when more than one male was present, all the males performed courtship displays, including Butterfly flights and Throat-flaggings, and they also moved nervously and rapidly between perches. In most cases males chased each other and we saw no copulations on these occasions.

Aggression.—We saw three types of aggressive behavior. Chases occurred mainly between males of all ages when they were together at a log. They could be very long (>1 min) in the vicinity of the log. These chases and displacements were very fast and most of the time we could not see if the individuals were banded, but on one occasion at log C1 we saw that the resident male was the individual who was chasing an intruder, and in two other occasions we saw adult males chasing immatures. We also saw groups of immature males present at the log and chasing each other in the absence of the resident.

Attack behavior was typical of the resident male at log B, although occasionally seen in others. This individual was very aggressive toward other birds (including hummingbirds and thrushes) that approached his territory around the log when he was alone. He would

rush suddenly toward them producing a low “grrraahh” or “cuaak” sound. However, he never attacked the other *C. leucorhoa* males that visited him early in the morning.

Displacements frequently occurred in the series of displays when there were several males present. A male could land and displace another on the log or on a nearby perch.

DISCUSSION

This study provides both new observations and confirmation of some previous ones on this species. Previous studies did not have the advantage of having such a large number of banded individuals; thus we were able to clarify several incongruencies, such as the ownership of logs, the identities and movements, and relations between nonresident or subordinate individuals, and the nature and possible role of groups of males at the display sites. We found that *C. leucorhoa* displays in loosely aggregated display territories or dispersed or exploded leks (Foster 1983, Prum 1994), although this is quite variable among individuals. Nevertheless, some of the display logs observed seemed to be visually or auditorily isolated from those of other males, as stated by Aldrich and Bole (1937). The mean distance between logs in a group and between groups of logs or leks was similar to what Théry (1992) found for *C. gutturalis* and Snow and Snow (1985) found for *Ilicura militaris*.

As Slud (1964) and Skutch (1967) observed, several juvenile and adult males may visit and display at the same log although according to our observations, they do not own or share the log permanently as stated by these authors. Rather, they are permitted to visit, especially at some times of the day, apparently as a social function related to establishment of a hierarchy as proposed by Foster (1983). Théry (1990) also found this to be the case in *C. gutturalis* in French Guiana. These visits also occur in *Ilicura militaris*, a group closely related to *Corapipo* according to Prum (1990, 1992) with which it shares several other display elements including the nonvocal “single snap or flop” in flight found during this study.

We found that each log belonged to a single resident male who spent most of his time in its vicinity and had priority for copulation with females. The most successful log (with

most female visits and one of the two copulations observed) also was the one with fewer male visits. This suggests that the establishment of a hierarchy, both by ritualized displays such as the warbling calls and the consecutive *Flap-chee-wahs*, and with more obvious aggressions such as chases, attacks and displacements, probably is the most important role of the multimale activity at the logs during the morning. The enhanced activity and sound also could make the logs more attractive to females. However, most female visits, including some that resulted in copulations, occurred when residents were alone, and our observation of a disruption could indicate that females avoided times when more than one male was present at the display site.

The early morning visits of numerous males could be a daily re-establishment of the hierarchy. This could reinforce the dominance of the resident males and assign a rank order to the visitors and put them in a “waiting list” to take over the log or logs that a group visits in case the resident disappears. The fact that some observers saw only single males (Aldrich and Bole 1937) or only groups (Slud 1964, Skutch 1967) displaying might be due to the times of day in which the observations were made. A similar peak of aggressive activity in early morning, with female visits and copulations later in the day, was found in Long-tailed Hermits (*Phaethornis superciliosus*; Stiles and Wolf 1979).

Prum (1986) found a similar situation of dominance by an individual and “moving” groups of male visitors in the White-throated Manakins in Suriname. Based on our banding data we demonstrated that these flocks were not permanent social assemblages, but of changing composition day to day. These data also permitted us to conclude that most individuals moved little between logs and then usually only for short distances.

The great variation found in spatial aggregation and activity schedules among the logs studied probably reflected different stages in the establishment of a hierarchy. Cluster C probably was in an early stage since it was not detected during previous years and there were high rates of male visitation and male-male interactions together with a low rate of female visits. Cluster A differed in that one of its logs (A1) had a well-established and suc-

successful resident while its neighbor (A2) was in an unstable situation in which the resident divided his time between two logs (A2 and A3). These tangential logs near A1 and C1 might be similar to the peripheral courts in which an intruder male *C. gutturalis* that often visited residents displayed erratically (Théry 1992). Log B, isolated during the mating season, might have had a highly aggressive male who had been effective in maintaining his dominance or the momentary situation in a system that changes considerably over time. Prum (1986) found in Suriname a similar localization of the logs in "loose groups" and "solitary situations" in *C. gutturalis*.

We do not know if the rapid sequences of *Flap-chee-wahs* performed by several males when present at the same log was the result of a coordinated display or if the "turns" they took displaying were simply to avoid crashing into each other; as Skutch (1967) observed, there otherwise was no coordination or synchronization present and males displayed simultaneously and independently at a log. The situation found in *C. leucorrhoa* in which several males engaged in possibly coordinated ritualized displays denotes similarity between *Corapipo* and *Chiroxiphia*, although in *Corapipo* there is no true cooperation in which the subordinate males contribute to the attraction of females to the group and more than one male is required in the display (Foster 1977). A close relationship between *Chiroxiphia* and *Corapipo* has been proposed by Brumfield and Braun (2001) based on electrophoretic methods. In *C. leucorrhoa*, visitors neither travel together nor visit the same log regularly, although they apparently do not move extensively in the area and remain in the vicinity of one established display site. Prum (1986) saw the same unsynchronized displays in *C. gutturalis*, although the groups of males moved together to nearby logs to continue with the displays. Brumfield and Braun (2001) also proposed *Antilophia galcata* to be closely related to *Corapipo*. Poorly known, *Antilophia* is the only manakin in which the lek or arena display behavior has been lost and males establish an extended pair bond with females, although they are highly aggregated and territorial (Marini and Cavalcanti 1993, Prum 1994), so far the only behavioral similarity found with *Corapipo*.

Various elements of the displays of *C. leucorrhoa* appear to be shared with *C. gutturalis* (Davis 1982; Prum 1986; Théry 1990, 1992), including the high trill or Advertising call, the *Flap-chee-wah* display, and the Canopy calls or Flight Song display. *C. gutturalis* possesses two displays not found in *C. leucorrhoa*: a posture in which they "raise their bill vertically and erect a small puff of white feathers at the base of the throat patch" (Prum 1986) and the displays in which they show the white wing patch (absent in *C. leucorrhoa*). Copulations in *C. leucorrhoa* seem to be very rare events, as also was observed by Théry (1990) in *C. gutturalis*. In both species copulation occurred when only one male was present (but see Davis 1949), and happened after a series of flights between perches in which the female could participate followed by a full sequence of a flight display and explosive landing on the log, the male jumping over the female before mounting her. However, in *C. gutturalis* the male landed facing away from the female, and in *C. leucorrhoa* the male landed facing her. In *C. leucorrhoa* the female did not touch the tips of the male's primaries with her bill as was seen in *C. gutturalis* before the three copulations observed by Théry (1990); we did not notice any possible signal of acceptance of copulation from the female. The low number of copulations in El Plástico also could be related to the low female:male ratio found in the area all year long, including the mating season (Rosselli 1994).

We found striking similarities between *C. leucorrhoa* and *Masius chrysopterus* (Prum and Johnson 1987), such as the countersinging or "nurrts" between the resident male and visitors. The Throat-flagging display, previously unknown in *Corapipo* (Prum 1994, Prum and Johnson 1987), seems very similar to the side-to-side bowing display of *Masius*. This, added to the similarity in the structure of the display calls and the fact that in *C. leucorrhoa* as well as in *Masius* some males display "faithfully" at a site in a territorial manner, while others are quite transient in their patterns, support Prum's (1990) phylogenetic analysis that places these genera close together.

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